

The effects of vegetative type, edges, fire history, rainfall and management in fire-maintained habitat

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Abstract. The combined effects of fire history, climate, and landscape features (e.g., edges) on habitat specialists need greater focus in fire ecology studies, which usually only emphasize characteristics of the most recent fire. Florida scrub-jays are an imperiled, territorial species that prefer medium (1.2-1.7 m) shrub heights, which are dynamic because of frequent fires. We measured short, medium, and tall habitat quality states annually within 10 ha grid cells (that represented potential territories) because fires and vegetative recovery cause annual variation in habitat quality. We used multistate models and model selection to test competing hypotheses about how transition probabilities vary between states as functions of environmental covariates. Covariates included vegetative type, edges (e.g., roads, forests), precipitation, openings (gaps between shrubs), mechanical cutting, and fire characteristics. Fire characteristics not only included an annual presence/absence of fire covariate, but also fire history covariates: time since the previous fire, the longest fire-free interval, and the number of repeated fires. Statistical models with support included many covariates for each transition probability, often including fire history, interactions and nonlinear relationships. Tall territories resulted from 28 years of fire suppression and habitat fragmentation that reduced the spread of fires across landscapes. Despite 35 years of habitat restoration and prescribed fires, half the territories remained tall suggesting a regime shift to a less desirable habitat condition. Edges reduced the effectiveness of fires in setting degraded scrub and flatwoods into earlier successional states making mechanical cutting an important tool to compliment frequent prescribed fires.

Key words: adaptive management; edges; fire; fragmentation; Florida scrub-jays; mapping; multistate; scrub; transition.

INTRODUCTION

Lightning-caused fire regimes have been major evolutionary drivers on nearly all continents (Tucker and Cadotte 2013), but the significance and management needs of biodiversity hotspots characterized by natural fire remain underestimated (Parr et al. 2014, Noss et al. 2015, Rundel et al. 2016). The North American Coastal Plain (NACP) has been subject to 70% habitat loss and has only been recently recognized as a global biodiversity hotspot that needs practical models to guide science-based fire management to restore and maintain its unique plants and animals (Noss et al. 2015). The Florida scrub-jay is an endemic bird confined to the Florida scrub and flatwoods ecosystem of the NACP and is an declining indicator species for habitat management (Noss et al. 1995, Coulon et al. 2010).

The natural fire regime of the scrub and flatwoods ecosystem has been greatly altered by humans (Duncan et al. 2009), as has occurred among fire adapted communities within the NACP and worldwide (Driscoll et al. 2010). The scrub and flatwoods ecosystem requires prescribed fire management to sustain biodiversity and prevent catastrophic wildfires from impacting human interests because anthropogenic landcover types (e.g., roads, cities) impede fire spread (Duncan and Schmalzer 2004).

The interactions among factors that influence the transitory dynamics of fire-maintained ecosystems are important to understand and manage to conserve biological diversity, but most studies focus only on habitat responses relative to the last fire (Nimmo et al. 2013). New approaches are needed to quantify spatial variation that results from repeated fires that do not burn all areas equally (Bradstock et al. 2005, Driscoll et al. 2010). Fire history seems may be particularly in scrub and flatwoods because repeated fires influence above-ground fuels characteristics (e.g., dead fuels above ground) and dominant plants depend on accumulated

below-ground biomass (roots, buds, starches) for sprouting after fire (Menges and Hawkes 1998).

Mechanical cutting is often needed to restore long unburned oak scrub because the habitat becomes difficult to ignite and support fire spread (Schmalzer and Boyle 1998). Evaluating ecosystem restoration usually involves comparing restoration sites to historical references, but one or a few reference sites often don't capture spatial and temporal variability (Kirkman et al. 2013). Restoration trajectories are often not linear or smooth; failure to understand alternative endpoints or exceptions to a deterministic trajectory can limit success (Matthews et al. 2009). Interactions between environmental variables (e.g., rainfall) and fire history have many effects on the direction and stochasticity of restoration trajectories (Zedler et al. 1983, Artman et al. 2001, Drewa et al. 2002, Clarke et al. 2014).

Variations in the intervals between fires can produce nonlinear relationships that are often described as memory or legacy effects (e.g., cavities, snags, stored underground biomass) (Ripplinger et al. 2015, Johnstone et al. 2016). Nonlinear relationships cause management thresholds in ecosystem state changes described by resilience theory (Ghermandi et al. 2010, Mori 2011, Johnson et al. 2013). Resilience theory commonly uses state-and-transition models that summarize ideas about how complex systems work through feedback loops, thresholds, and triggers (Bagchi et al. 2012, Ratajczak et al. 2014).

Multistate models are new approaches to empirically quantify ecosystem dynamics by measuring states and using generalized linear models to estimate how environmental covariates influence transition probabilities between states (Breininger et al. 2010, Veran et al. 2012, Zweig and Kitchens 2014). We previously used multistate models and multimodel inference to quantify scrub and flatwoods habitat transition probabilities of potential Florida scrub-jay territories at 5-

year intervals (1994-2004) using combinations of environmental factors that focused on vegetation type, edges, and management actions as covariates (Breininger et al. 2010). We used landscape units that defined potential Florida scrub-jay territories because transition probabilities within potential territories provide the parameters to predict how alternative management actions can be used to better manage and restore the scrub and flatwoods ecosystem (Williams et al. 2011).

Here we use multistate modeling and multimodel inference to predict how annual habitat state transition probabilities (2004-2015) are influenced by environmental covariates important in previous studies and new environmental covariates that incorporate information on fire history, rainfall and open sandy areas. These new covariates were described as important in many ecosystem studies and likely to be influential in early successional state transitions, which dominated historical scrub and flatwoods landscapes (Duncan et al. 2004, Duncan et al. 2009). Our approach for applying habitat states (short, medium, tall) for potential territories does not consider all elements of Florida scrub-jay habitat quality (Burgman et al. 2001). However, characterizing landscape units into these states is practical to conduct across broad geographic areas annually and is useful for adaptive management (Johnson et al. 2011). Nearly 30 years of data on demography and dispersal shows that short and tall states are population sinks where mortality exceeds recruitment and the medium state is a source where recruitment exceeds mortality (Breininger et al. 2014b). Although in other studies we have subdivided the medium state into open and closed based on the amount of open sandy area between shrubs, here, we focused on states defined entirely by height because we lacked enough samples to study how many factors influence open state dynamics. However, we tested whether openings are an important covariate influencing height state dynamics because openings can, for example,

influence fire spread as open sandy areas cause discontinuity in fuels (Schmalzer 2003, Menges et al. 2008, Duncan et al. 2015). Fires in scrub can also spread poorly depending on meteorological conditions such as soil and fuel moisture that can be influenced by rainfall (Adrian 2006) and thus a rapidly changing climate is likely to further impact disturbance regimes (Turner 2010, Foster et al. 2017).

Our primary objective was to test a competing model set to investigate whether a few simple covariates or many covariates best describe transition probabilities in scrub and flatwoods, including models with interactions and nonlinear effects. We also compare new state abundance trends with predictions (Breininger et al. 2010) and use new transition probability estimates to predict future trends of restoration success. Our final objectives include quantifying trends in management effort based on the number of potential territories burned and cut each year.

METHODS

Study system

Our study was conducted on Kennedy Space Center/Merritt Island National Wildlife Refuge (KSC/MINWR), a barrier island complex located along central Florida's Atlantic Coast. Oak scrub and flatwoods are heterogeneous vegetative communities dominated by scrub oaks, saw palmetto, grasses and ericaceous plants. Cover of scrub oaks is greatest on the most well-drained soils ("oak") and declines on moderately drained soils ("flatwoods") where the more flammable flatwoods species increase. Although considered distinct plant communities, oak and flatwoods are often termed scrubby flatwoods when they are intermixed within fire management units

(Breininger et al. 2002). Plant composition changes little after fire because most plants are clonal and re-sprout within weeks (Schmalzer and Hinkle 1992).

Scrub and flatwoods ecosystems on KSC/MINWR had many openings and little forest prior to a fire suppression period (1950-1978), which caused a loss of openings and increases in tall shrubs and forests (Duncan et al. 1999). Marshes are extensively intermingled within scrub and flatwoods, but many of these became hardwood swamps during the fire suppression period. A subsequent prescribed fire program focused on fuels management as part of a national program to reduce threats of catastrophic fires on human interests. Getting the ecosystem back to short and medium habitat states has been difficult, as tall shrubs and forests burn poorly and mechanical cutting is generally needed to reintroduce fire into degraded areas (Schmalzer and Boyle 1998). Currently, the fire return interval in a management unit can be as often as 3-5 years, but specific patches may burn only every 14 years or longer (Duncan et al. 2009).

Data collection

The study area was delineated by 695 10-ha square polygons that approximate all potential Florida scrub-jay territories. Florida scrub-jay territories average 10 ha when habitat is fully saturated by Florida scrub-jays; studying the dynamics of potential territories is useful because most Florida scrub-jay populations have declined by >50% leaving much potential habitat unoccupied (Breininger et al. 2006). These 695 potential territories represented all potential habitat within areas managed using prescribed fires, while excluding habitat fragments that were no longer managed or relatively isolated scrub patches that had minimal contribution to the Florida scrub-jay population (Carter et al. 2006).

We measured habitat states (short, medium, tall) described below each year from 2004-2015 using 1.0 m resolution aerial photography. Field observations supplemented state estimation because most potential territories were within long-term demographic study sites where we uniquely mark and resight Florida scrub-jays (Breininger et al. 2009, Breininger et al. 2010). Years were defined as April 1 to March 31 corresponding to Florida scrub-jay nesting season and the timing of most aerial photographs. Short territories have many openings between shrubs, medium has a uniform (flat) appearance and tall shows texture on images because tall shrubs produce shade. Short lacks shrubs > 1.2 m tall and experienced a recent (< 5 years), extensive burn. Medium and tall territories often had heterogeneous shrub heights because fires in oak and flatwoods often burn in mosaic patterns so that potential territories include patches of vegetation with different fire histories. Long-term demographic research that defined these criteria were based on having enough medium shrubs to support recruitment that exceeded mortality, but not too many tall shrubs that caused Florida scrub-jay territories to have mortality that exceeded recruitment across a range of population densities. Medium includes at least 0.4 ha of shrubs 1.2-1.7 m tall (optimal height) and excludes large patches (>1.0 ha) of tall shrubs (>1.7 m tall). Tall includes areas with > 1.0 ha of tall shrubs (Breininger et al. 2010). On average it takes 8 years without disturbance for oaks to reach medium height and 20 years for scrub to become tall (Schmalzer and Hinkle 1992, Duncan et al. 1995).

We identified a suite of covariates predicted to influence the transition probabilities between habitat states. The static (non-time varying) covariate “oak” identified potential territories intersecting well-drained soils, and “flatwoods” identified potential territories that included moderately drained soils with smaller patches of oaks than are found on well-drained soils. The static covariate “edge” recorded whether a man-made or forest edge intersected a potential

territory. The dynamic (time-varying) covariate “open” was a categorical variable that distinguished whether scrub in potential territories was open (>50% or area had open sandy gaps between shrubs) or closed (few gaps). The dynamic covariate “cutting” distinguished territories where at least ¼ of the territory was subject that year to mechanical cutting of trees and shrubs.

The fire history of territories differed across the KSC/MINWR landscape; in order to encompass these differences we incorporated several dynamic covariates related to the fire histories that we predicted had an influence on transition probabilities. The dynamic covariate “fire” distinguished territories where at least ¼ of the territory burned that year based on remote sensing and fire records (Shao and Duncan 2007). We chose 3 fire history variables that reflected different hypotheses about how fire history would affect habitat transitions that we predicted to be uncorrelated with fire and each other. The first fire history covariate time-since-fire, “TSF”, represented the number of years without fire prior to the current interval and therefore independent of “fire” during the current interval. We selected TSF because growth is more rapid soon after fires and then slows (Schmalzer 2003). The second fire history covariate longest fire interval, “LFI”, represented the longest period without fire during the previous 20 years, recognizing that fire free intervals approaching 20 years result in states resilient to fire (Duncan et al. 1999). The third fire covariate “NF” included the number of fires for the previous 10 years because repeated, short-interval fires can deplete underground biomass (Saha et al. 2010).

The dynamic covariate standardized precipitation index, “SPI”, was obtained from Florida climate division 3 from the National Climatic Data Center, Asheville, NC (www.ncdc.noaa.gov/). The SPI describes the observed precipitation over a time period as the number of standard deviations above or below the long-term mean precipitation for that time period (McKee et al. 1993) and has been useful in studying responses in scrub vegetation

(Foster et al. 2014, 2015). We used the 12-month SPI for April – March 31 as a measure of drought. The 12 month SPI for March compares the cumulative precipitation from the previous April to the current March to the historic pattern of precipitation for that time period.

Data analyses

We used multistate models to analyze annual transition probabilities between states (Fig. 1) as a multinomial model of static and dynamic environmental covariates. Static variables were oak/flatwoods and edge/no edge. One dynamic variable (SPI) was the same for all potential territories, but unique to each interval. Other dynamic variables were specific to each interval and potential territory: fire/no fire, mechanical cutting/no cutting, openings/no openings, 3 fire history variables.

Each multistate model consisted of a likelihood combining 3 multinomials, 1 for each of the 3 states. We estimated transition probabilities for state changes (e.g., short-to-medium); transition probability estimates of states remaining the same between years (e.g., short-to-short) were estimated by subtracting the transition probability estimates of state changes from 1.0. The transition of short-to-tall was constrained to zero because it didn't occur, which enhanced numerical estimation. We developed 40 competing models representing hypotheses of how combinations of different variables, two-way interactions, linear and quadratic relationships would affect state transitions. Models were implemented in Program Mark (White et al. 2006), which produced an AIC_c model-selection table, estimates of β s (regression parameters), and transition probabilities along with their precision (i.e., SE and CI). We made *a priori* predictions about the direction for each β , similar to the previous modeling in order to represent specific ecological hypotheses for each transition probability (Breininger et al. 2010).

We used a simple approach to present how state transitions (and measures of precision) varied annually based only on plant composition (oak versus flatwoods), excluding environmental covariates because oak and flatwoods are often considered distinct plant communities. We also predicted future abundances of each state for the next 12 years by Markov projections, beginning with the 2015 vector of state abundances, as we did previously (Breininger et al. 2010). The Markov matrices for the future predictions were estimated with time constant models, separately for oak and flatwoods without other environmental covariates (Breininger et al. 2010). To determine if there were trends in management effort, we used linear regression of the number of grid cells burned (1983-2015) and cut (2004-2015) for time periods with data on these management efforts.

RESULTS

No simple models that included only vegetation type (oak/flatwoods) or habitat management actions (fire/no fire, cutting/no cutting) had support, whereas 6 more complicated models had > 99% of the empirical support (Table 1). There was much similarity amongst the top models, but differences among transition probabilities regarding which covariates were important. Models with support included all covariates that were previously important (oak, edge, fire, and cutting) and new covariates involving fire history (time-since-fire, longest fire free interval, number of fires in previous 10 years, openings) and annual rainfall (standardized precipitation index).

Table 2 compares our *a priori* predictions with results for all covariates important in the best supported model. We presented only the best model because other top models were similar and β 's absent in the top model involved interactions that had standard errors many times greater than mean estimates. The best model had mean β 's with CI's that overlapped zero, but excluding these effects during *post hoc* analyses produced models without AIC_c support. The main effect

for β 's describing the oak versus flatwoods often had CI that overlapped zero, but we included the oak versus flatwoods effect because all supported models included an oak versus flatwood effect, and many covariates had different effects depending on whether the site was oak or flatwoods (Table 2). All supported models had an effect for whether fire occurred in the current interval, but the CI's overlapped zero for transitions from earlier to later successional states.

Every transition probability included an edge effect; β 's representing covariates in the best model usually had the same direction of effects that we predicted, except for the number of fires in the previous 10 years. The negative β 's for openings clarified the effect where authors disagreed on *a priori* predictions. Supported models included many covariate effects for transitions between short-to-medium, medium-to-short and for medium-to-tall, which were transition probabilities that previously had low sample sizes and therefore limited our abilities to test many covariate effects. In this study, transitions from short and medium to other states were more common because the states had greater relative abundances, and we estimated transition probabilities from 11 annual intervals versus 3 5-year intervals (Breininger et al. 2010).

The fire history TSF affected transitions from earlier to later successional states, with a nonlinear effect for short-to-medium. Other fire history covariates (NF and LFI) often had weak effects (small β 's) with uncertain directions (CI overlapped zero). Fire history covariates were not highly correlated ($r^2 < 0.4$) and post hoc analyses to remove covariates from models with multiple fire history covariates did not improve model support or change directions of the β estimates of fire history covariates, as can occur when covariates are highly correlated (Zuur et al. 2010). Each of the 3 covariates was chosen for a different *a priori* mechanism that might affect transition probabilities (e.g., nonlinear growth, underground biomass depletion, developing inflammable above ground fuels structure) and eliminating 1-2 fire history covariates in *post hoc*

analyses resulted in models that had no support compared to the top models indicating that the fire history covariates provided different information, albeit with comparably weak effects and poor precision.

Precipitation did not influence transitions to a later successional state (growth) but influenced transitions to an earlier successional state and in oak. The quadratic relationship occurred because transition probabilities peaked at low to medium drought conditions being lowest during severe droughts (when prescribed fires are not allowed) or when rainfall was average or greater.

All habitat states were widely distributed throughout the landscape (Figure 2), and tall territories remained the most abundant habitat state (Figure 3). Tall territories declined and medium (optimal) territories increased confirming predictions made from the earlier model (Breininger et al. 2010). Our use of Markov processes to generate a vector of state abundances predicted almost no change in state abundances across the next 12 years versus a continued tall state decrease and medium state increase as predicted from the earlier data (Breininger et al. 2010). There was a slight increase in the number of grid cells burned each year and no trends in cutting. Cutting only occurred in <25 grid cells each year, except for 2006 and 2011 (Figure 4).

Transitions probabilities from tall to earlier successional states were usually among the smallest and annual transition probabilities varied greatly, especially for short-to-medium which generally had the greatest transition probabilities between states (Table 4). Transition probabilities to earlier successional states were greatest during the greatest droughts (2007-2008, 2011-2012).

DISCUSSION

Multistate models provided a unifying modeling framework to empirically quantify the effects of many environmental variables on habitat dynamics, by breaking a large landscape into potential territories and developing a longitudinal history of states and environmental covariates. No simple model explained habitat dynamics, as all models with empirical support included many environmental factors for each transition probability; these effects included interactions and nonlinear relationships, which are common in fire ecology studies (Driscoll et al. 2010). Results expanded previous work (Breininger et al. 2010) identifying complex interactions between covariates, and many new covariate effects (fire history, precipitation, openings) for many transitions (e.g., short-to-medium, medium-to-short, medium-to-tall).

Restoration and management actions (e.g., fire, cutting) had important effects, but environmental factors often had greater effects on transition probabilities (e.g., edge effects on tall-to-medium: Table 2). Edges (roads and forests), primarily resulting from anthropogenic factors, were among the most influential factor across transition probabilities; these strong effects made sense because edges disrupt fire spread (Duncan and Schmalzer 2004). Forests were relatively rare in the historical landscapes and resulted from reductions in fire frequency from natural fire regimes causing low flammability (Duncan et al. 1999, Duncan et al. 2004). Habitat fragmentation typically increases ignitions and fire spread in other ecosystems, but still has detrimental impacts (Kraaij et al. 2013).

Cutting was an important management action influencing transitions because tall scrub had become resistant to fire, and cutting along edges and frequent fire appear to be the only solution to Florida scrub-jay population recovery on KSC/MINWR (Johnson et al. 2011). We agree with colleagues that mechanical cutting is not a replacement for fire, and care is needed to avoid the

spread of exotics and reducing the cover of species important for spreading fires (Schmalzer and Boyle 1998, Menges and Gordon 2010).

Fire history effects were practical to study in our system because fires occurred every few years instead of decades, or longer. The presence/absence of fire during an annual interval usually had a larger effect than fire history variables, except that time since fire (TSF) had a great effect for the short-to-medium transition in oak. The presence/absence of fire might have had a lesser impact than TSF because short scrub generally lacks enough fuels to burn extensively. The TSF nonlinear effect could be explained by growth being most rapid a few years after fire (Schmalzer and Hinkle 1992).

We predicted stronger effects from other fire history covariates, especially for the length of the fire free interval (LFI) because scrub is difficult to restore once it is unburned for ≥ 20 years. We expected that LFI would be important because increasing underground biomass allows for more rapid regrowth after fire (Maliakal et al. 2000, Boughton et al. 2006). One explanation for only small fire history effects might be that the effects of fire history on vegetation might have occurred at a smaller geographic scale than potential territories, which would have had heterogeneous fire histories. The number of fires (NF) decreased tall-to-short and tall-to medium transitions contradicting our *a priori* hypothesis, but the effect was poorly estimated (CI overlapped zero). One explanation might be that it takes at least 3-5 years for enough fuels to accumulate to carry fire and greater fuel levels might be needed for fires to burn severely enough to spread into tall scrub patches. Another explanation is that fires did not burn often enough to deplete underground biomass because there were not enough grasses to carry frequent fire (see below).

Fire severity can be an important habitat covariate (Lindenmayer et al. 2013, Fang et al. 2015), but can be challenging to measure and is often related to fire size (Miller et al. 2009, Cansler and McKenzie 2014). We are investigating methods to develop longitudinal fire severity histories across our study sites and acknowledge that lack of fire severity data is an important limitation. However, management objectives in our study sites often do not include severe fires because of the proximity to cities and space program facilities and the negative impacts of extensive fires to Florida scrub-jay survival (Breininger et al. 2009).

Historical benchmarks or reference conditions are often used to evaluate progress towards habitat recovery, however, these should include spatial and temporal variability (Kirkman et al. 2013). In addition to edge effects, we suspect that fire spread today often differs from historical conditions because prescribed fires vary in seasonality and meteorology with natural, lightning ignited fires (Duncan et al. 2009). There are many vegetative differences in the flammability within landscapes, and grasses are especially important for spreading fire (Breininger et al. 2002). The growth and flowering of many important grass species (e.g., *Aristida stricta* var. *beyrichiana*) is dependent on fires that occur at the transition between the dry and thunderstorm seasons when most lightning fires occurred (Platt et al. 1988, Noss 2013).

The Pre-European landscape might have been resilient to change because frequent lightning fires could spread easily through grasses among short and medium territories that lacked roads and forests to impede fire spread (Duncan et al. 1999). Early landscapes had many open sandy areas, which usually disappear within 1-2 years after fire in recent times (Schmalzer and Hinkle 1992). The negative relationship we observed between in open scrub and the transition from medium-to-tall might have occurred because open scrub was an indicator of slower growth. Slower growth might have resulted from site differences (e.g., topography) or fire severity.

Anthropogenic effects often produce alternative states that are resistant to change or states that are unstable (Scheffer and Carpenter 2003, Larson et al. 2013, Johnstone et al. 2016). Following 28 years of fire suppression, 35 years of prescribed fires only reduced slightly the extent of tall territories that had become resistant to restoration. Other complications included restrictions on prescribed fires that must be ignited under particular wind directions to avoid smoke impacts to smoke sensitive areas. These restoration challenges occur across the geographic region making many small Florida scrub-jay populations vulnerable to extinction (Duncan et al. 2004, Breininger et al. 2006).

Restoration programs often focus on conducting enough management to get past a threshold that alters system behavior, removing feedback loops that lead to a degraded state, and enhancing feedback loops that produce a desired stable state (Suding 2011). Burning during the best season to stimulate grasses and promote fire spread might be advantageous, but fire managers in our study sites had extreme limitations regarding meteorological and operational constraints that made burning only during the dry-to-wet transitional season (e.g., May) difficult. Cutting was an expensive tool, and it may be unreasonable to remove most forest edges and edges associated with human landscape features so that prioritization of management efforts becomes necessary. We have observed many habitat and population management restoration successes in particular landscapes, but most conservation areas are at less than half Florida scrub-jay carrying capacity (Breininger et al. 2006). Population modeling and Florida scrub-jay sociobiology suggest that habitat management prioritization might focus on maintaining the largest populations because population recovery can be slow, especially when there are not large numbers of nonbreeding individuals (Breininger et al. 1999, Breininger et al. 2014b).

Funding for prescribed fires often focuses on maximizing fuels reduction allowing fuels to accumulate until fires can burn them extensively, causing potential Florida scrub-jay territories to have a large sink (short, tall) to source (medium) habitat ratio, as occurred herein. We believe “optimal habitat management” might be better at reducing catastrophic fire risk than fuels management in priority areas (Breininger et al. 2014a). In an optimal habitat management strategy, prescribed fires would be initiated sooner than a fuels reduction strategy by attempting prescribed fires before all fuels are likely to ignite thus creating transitory openings and heterogeneity among shrub patches at the territory scale. In habitat occupied by Florida scrub-jays near carrying capacity, optimal habitat management would attempt mosaic fires to provide some unburned patches to serve as nest sites, provide acorns, and areas to escape predators. Such fire mosaics would require greater post-fire monitoring because unburned patches might reignite. Fire modeling suggests this strategy would reduce fuels continuity decreasing the risk of spreading potentially catastrophic fires (e.g., wildfires) that are expensive to control (Duncan et al. 2015). In our view, waiting until fuels accumulate to levels that support complete fires increases the risks of catastrophic wildfires between controlled fires. Frequent and severe fires could be conducted in unoccupied Florida scrub-jay habitat in an attempt to set the system back into an earlier successional state associated with historical conditions promoting population recovery in those areas at a later date.

Our study does not take into account the effects of a changing climate; however, it is likely that the areal extent of oak and flatwoods will be reduced with rising sea levels putting pressure on managing biodiversity in increasingly smaller areas (Foster et al. 2017). Changes in precipitation might include heavier precipitation events and longer periods between precipitation events; droughts may become more frequent (Karl et al. 2009). We observed the effects of SPI

on oak transitions to earlier successional states were not linear because drought promotes fire spread, but extreme droughts force a shutdown of prescribed fire because of increased catastrophic fire risk. Droughts might not have effected flatwoods because the vegetation is more flammable and the water table closer to the root zone (Schmalzer and Hinkle 1992).

Scientists need to broaden study implications, but generalizations also lead to debates as to whether Florida scrub-jays, for example, should be a scrub management indicator for all scrub (Menges and Gordon 2010). A nuanced approach could consider regional biodiversity where opportunities for conservation vary among species and conservation areas. In our study region, conservation opportunities are limited by urbanization and species geographic differences (Duncan et al. 2004). Most species of conservation concern in our study site benefited by conditions best for Florida scrub-jays, and we know of no species of conservation concern that would decline from Florida scrub-jay management directed at one of the species last remaining extant large populations.

Plant ecologists recommend pyrodiversity to account for the requirements of lesser known species while animal ecologists have increasingly questioned whether pyrodiversity creates faunal biodiversity (Parr and Andersen 2006, Menges 2007, Clarke 2008, Farnsworth et al. 2014). Our study site had great pyrodiversity was of poor habitat quality for Florida scrub-jays because of too much tall scrub. Rather than simple statistical distributions, fire frequency should be based on species biology (Gill and McCarthy 1998, Kelly et al. 2015), such as habitat and population state (Johnson et al. 2011, Williams et al. 2011). Optimal Florida scrub-jay territories in our study area includes a specific fire mosaic because openings disappear a few years after fire and medium height scrub on average is 8-20 years post fire (Breininger et al. 2014b).

Long-term studies have shown geographic differences in vegetative response to fire and fire return rates (Menges et al. 2008). Depth to water table, nutrient availability, and the geological age of soils help explain these geographic differences (Schmalzer and Hinkle 1992). Focusing on broad scale approaches does not always consider spatial and temporal complexities and fine scale habitat features important to endemic species (Bond and Parr 2010, Watson et al. 2011, Noss et al. 2015). A strength of our study is demonstrating that a monitoring approach can evaluate how management and environmental factors interact to effect habitat quality while being site-specific.

Monitoring is often most effective when it informs decision making (Williams et al. 2002, Nichols and Williams 2006). The transition probabilities estimated herein can be updated through monitoring to drive management decision models (Johnson et al. 2011, Williams et al. 2011) and link habitat quality to population predictions (McCarthy and Thompson 2001, Akcakaya et al. 2004, Burgman et al. 2005, Duarte et al. 2016). Multistate modeling enhanced the ability to examine relationships among environmental factors and fire history, as such relationships have been understudied (Haslem et al. 2012, Levick et al. 2015). Quantification of progress towards desired conditions that incorporates the ability to account for spatial and temporal variability might be more useful than simple comparisons with historical benchmarks or reference sites (Kirkman et al. 2013).

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Table 1. Model selection table for top 6 models (AICc weight > 0.01) of the 40 *a priori* models.

Model	Transition probabilities (ψ) affected by different covariates under top-supported models						Model selection results			
							Delta	AICc	No.	Deviance
	Longest fire interval	SPI \times Fire	Openings	Openings \times Oak	Number fires	Number fires \times Oak	AICc	Weight	parameters	
1	$\psi^{SM} \psi^{TS} \psi^{TM}$		ψ^{MT}		$\psi^{TS} \psi^{TM}$		0.00	0.44	45	4420
2	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		ψ^{SM}	ψ^{MS}		$\psi^{TS} \psi^{TM}$	1.39	0.22	50	4411
3	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		ψ^{MT}				1.67	0.19	42	4427
4	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		$\psi^{SM} \psi^{MT}$	ψ^{MS}			3.72	0.07	48	4417
5	$\psi^{SM} \psi^{TS} \psi^{TM}$	$\psi^{MS} \psi^{TS} \psi^{TM}$	ψ^{MT}		$\psi^{TS} \psi^{TM}$		5.19	0.03	55	4405
6	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		$\psi^{SM} \psi^{MT}$		$\psi^{TS} \psi^{TM}$		5.25	0.03	52	4411

Superscripts refer to particular transition probabilities between states ^S = short, ^M = medium, ^T = tall. All top models included the effects of edge and oak \times fire for all ψ . All top models included a quadratic relationship for time since fire (TSF) in oak for ψ^{SM} ; the covariate TSF was not supported in flatwoods when predicting ψ^{SM} . All top models included a linear TSF effect for ψ^{MT} . The effect

of SPI (standardized precipitation index) applied only to oak for ψ^{MS} , ψ^{TS} , ψ^{TM} among the top models. The effect of cutting applied only to ψ^{MT} , ψ^{TS} , and ψ^{TM} for top models.

Table 2. Comparing estimated regression slopes (β 's) with *a priori* predictions for the best habitat transition model.

Transitions (ψ)	β description	β	Lower CL	Upper CL	<i>A priori</i> prediction	Explanation
ψ^{SM}	Flatwoods vs oak	-1.12	-1.93	-0.32	-	Agreement, flatwoods more likely to burn extensively
ψ^{SM}	Edge	0.41	0.12	0.70	+	Agreement, edges reduce fire spread
$\psi^{\text{SM oak}}$	Fire vs no fire	-0.11	-0.77	0.56	-	Agreement (but CI overlapped 0.0), fires reduce height
ψ^{SM} flatwoods	Fire vs no fire	-1.56	-2.36	-0.76	-	Agreement, fires reduce height
$\psi^{\text{SM oak}}$	TSF	0.48	0.26	0.70	+	Agreement, growth after fire
$\psi^{\text{SM oak}}$	TSF squared	-0.02	-0.03	-0.01	-	Agreement, growth rapid immediately after fire than slows
ψ^{SM} flatwoods	TSF	1.01	0.66	1.36	+	Agreement, growth after fire
ψ^{SM} flatwoods	TSF squared	-0.08	-0.12	-0.05	-	Agreement, growth rapid immediately after fire than slows

ψ^{SM}	LFI	0.04	0.01	0.07	+	Agreement, longer fire intervals allow faster regrowth
ψ^{MS}	Flatwoods vs oak	0.05	-1.04	1.14	+	Agreement (but CI overlapped 0.0), we predicted flatwoods more likely to burn extensively
ψ^{MSoak}	Edge	-0.78	-1.22	-0.35	-	Agreement, edges reduce fire spread
ψ^{MSoak}	Fire vs no fire	3.38	2.51	4.24	+	Agreement, fires reduce height
$\psi^{MSflatwood}$ s	Fire vs no fire	3.72	2.96	4.49	+	Agreement, fires reduce height
ψ^{MSoak}	SPI	-1.17	-1.79	-0.54	-	Agreement, fire spread increases in drought for oak
ψ^{MSoak}	SPI squared	-1.49	-2.04	-0.95	-	Agreement, no prescribed fire in extreme drought
ψ^{MT}	Flatwoods vs oak	0.06	-0.27	0.39	+	Agreement (but CI overlapped 0.0), we predicted flatwoods recovers faster than oak
ψ^{MT}	Edge	1.07	0.74	1.39	+	Agreement, edges reduce fire spread
$\psi^{MT\ oak}$	Fire vs no fire	-0.58	-1.11	-0.05	-	Agreement, fires reduce height
ψ^{MT} flatwoods	Fire vs no fire	-0.24	-0.80	0.31	-	Agreement (but CI overlapped 0.0), fires reduce height
ψ^{MT}	TSF	0.06	0.01	0.11	+	Agreement, growth after fire
ψ^{MT}	Cutting	-2.09	-4.07	-0.11	-	Agreement, mechanical cutting decreases height

$\psi^{MT\ oak}$	Openings	-1.46	-1.94	-0.97	+ and -	Clarification, open areas suggest slow shrub recovery
ψ^{TS}	Flatwoods vs oak	0.91	-0.49	2.30	+	Agreement (but CI overlapped 0.0), we predicted flatwoods more likely to burn extensively
$\psi^{TS\ oak}$	Edge	-1.36	-1.83	-0.90	-	Agreement, edges reduce fire spread
$\psi^{TS\ oak}$	Fire vs no fire	3.94	2.67	5.22	+	Agreement, fires reduce height
$\psi^{TS\ flatwoods}$	Fire vs no fire	3.42	2.73	4.11	+	Agreement, fires reduce height
$\psi^{TS\ oak}$	Cutting	2.19	1.63	2.75	+	Agreement, mechanical cutting decreases height
$\psi^{TS\ oak}$	SPI	-1.07	-1.89	-0.25	-	Agreement, fire spread increases in drought
$\psi^{TS\ oak}$	SPI squared	-1.12	-1.72	-0.51	-	Agreement, no prescribed fire in extreme drought
ψ^{TS}	Number fires	-0.17	-0.43	0.09	-	Disagreement (but CI overlapped 0.0) , we predicted more fires increase recovery
ψ^{TS}	LFI	-0.03	-0.07	0.01	-	Agreement (but CI overlapped 0.0) , longer fire intervals slow restoration to earlier states
ψ^{TM}	Flatwoods vs oak	1.50	-0.21	3.21	+	Agreement (but CI overlapped 0.0), we predicted flatwoods more likely to burn extensively
$\psi^{TM\ oak}$	Edge	-0.71	-1.21	-0.21	-	Agreement, edges reduce fire spread
$\psi^{TM\ oak}$	Fire vs no fire	4.50	3.08	5.92	+	Agreement, fires reduce height

ψ^{TM} flatwoods	Fire vs no fire	3.48	2.55	4.42	+	Agreement, fires reduce height
ψ^{TM}	Number fires	-0.25	-0.51	0.01	-	Disagreement (but CI overlapped 0.0), we predicted more fires increase transitions to earlier successional states
ψ^{TM}	LFI	-0.09	-0.13	-0.04	-	Agreement, longer fire intervals slow restoration to earlier states
ψ^{TM}	Cutting	0.62	-0.08	1.32	+	Agreement (but CI overlapped 0.0), mechanical cutting decreases height
$\psi^{\text{TM oak}}$	SPI	-0.87	-1.54	-0.20	-	Agreement, fire spread increases in drought
$\psi^{\text{TM oak}}$	SPI squared	-0.01	-0.52	0.50	-	Agreement, droughts have biggest effect

Transition probability superscripts were SM for short to medium, MS for medium to short, MT for medium to tall, TS for tall to short, TM for tall to medium. Superscripts that included oak had a β specific to oak, superscripts that included flatwoods had a β specific to flatwoods and superscripts without oak or flatwoods had a single β for both oak and flatwoods transitions. Abbreviations TSF = Time-since-fire, LFI = longest fire interval, SPI = standardized precipitation index. Nonlinear relationships were represented by a squared term (quadratic).

Table 3. Annual transition probability estimates (95% CI).

year	short-medium	medium-short	medium-tall	tall-short	tall-medium
scrub					
2004-2005	0.57(0.45-0.68)	n/a	0.18(0.12-0.26)	0.00(0.00-0.03)	0.01(0-0.04)
2005-2006	0.71(0.53-0.84)	0.04(0.02-0.09)	0.29(0.22-0.37)	0.01(0.00-0.04)	n/a
2006-2007	0.22(0.09-0.46)	n/a	0.09(0.05-0.16)	0.00(0.00-0.03)	0.01(0.01-0.04)
2007-2008	0.40(0.19-0.65)	0.28(0.21-0.37)	0.03(0.01-0.08)	0.08(0.05-0.11)	0.03(0.01-0.05)
2008-2009	0.19(0.11-0.31)	0.02(0.01-0.08)	0.05(0.02-0.12)	0.01(0-0.03)	0.03(0.01-0.06)
2009-2010	0.13(0.06-0.25)	0.01(0.00-0.07)	0.04(0.01-0.1)	n/a	n/a
2010-2011	0.48(0.34-0.62)	0.05(0.02-0.11)	0.15(0.09-0.23)	0.04(0.02-0.08)	0.03(0.02-0.06)
2011-2012	0.46(0.32-0.61)	0.06(0.03-0.12)	0.07(0.03-0.13)	0.03(0.02-0.06)	0.14(0.11-0.19)
2012-2013	0.24(0.13-0.41)	0.08(0.05-0.14)	0.02(0.01-0.06)	n/a	0.00(0.00-0.03)
2013-2014	0.12(0.05-0.26)	n/a	0.02(0.01-0.06)	n/a	n/a
2014-2015	0.17(0.08-0.32)	0.01(0.00-0.05)	0.07(0.04-0.12)	n/a	0.01(0-0.04)
flatwoods					
2004-2005	0.54(0.66-0.54)	0.09(0.04-0.20)	0.31(0.21-0.45)	0.08(0.05-0.13)	0.01(0-0.05)

2005-2006	0.38(0.26-0.52)	0.10(0.05-0.19)	0.31(0.21-0.42)	0.01(0.00-0.04)	n/a
2006-2007	0.23(0.12-0.39)	0.05(0.02-0.14)	0.21(0.13-0.33)	0.03(0.01-0.06)	n/a
2007-2008	0.16(0.07-0.31)	0.16(0.09-0.29)	0.11(0.05-0.22)	0.07(0.04-0.12)	0.01(0.00-0.04)
2008-2009	0.15(0.07-0.26)	0.15(0.07-0.28)	0.06(0.02-0.18)	0.03(0.01-0.06)	0.04(0.02-0.08)
2009-2010	0.12(0.06-0.23)	n/a	0.02(0.00-0.12)	n/a	n/a
2010-2011	0.44(0.31-0.58)	0.02(0.00-0.11)	0.12(0.06-0.23)	0.01(0.00-0.04)	0.01(0.00-0.04)
2011-2012	0.25(0.13-0.43)	0.17(0.10-0.28)	0.03(0.01-0.1)	0.12(0.08-0.18)	0.10(0.06-0.15)
2012-2013	0.10(0.05-0.21)	0.22(0.15-0.32)	0.01(0.00-0.08)	0.04(0.02-0.09)	0.07(0.04-0.12)
2013-2014	0.08(0.03-0.16)	n/a	0.07(0.03-0.15)	n/a	n/a
2014-2015	0.25(0.16-0.36)	0.11(0.06-0.2)	0.11(0.06-0.20)	0.08(0.05-0.14)	0.07(0.04-0.13)

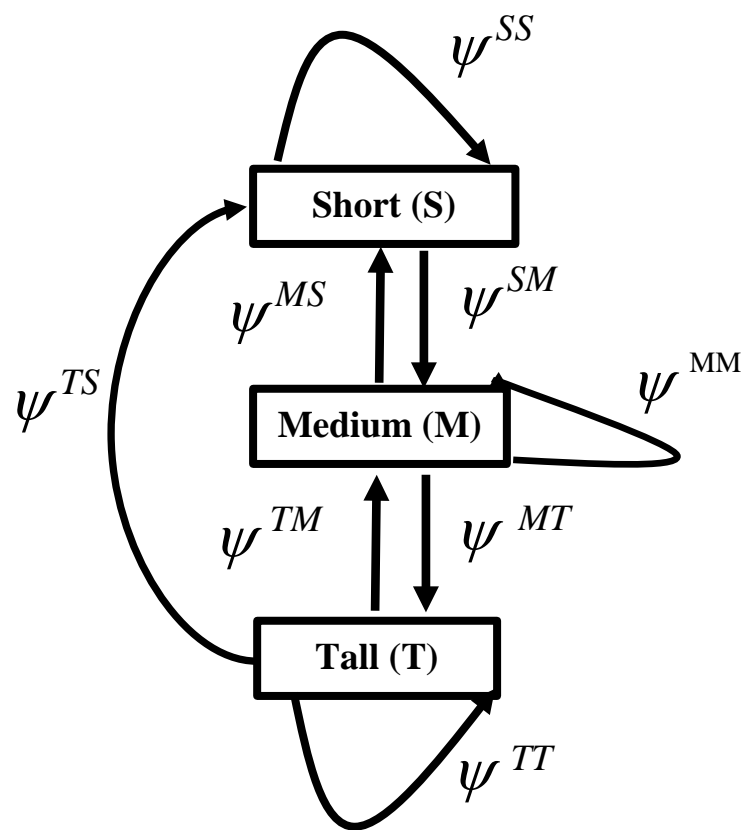
n/a = annual transitions that did not occur

Figure 1. Habitat quality states and transition probabilities (ψ) where superscripts sequentially indicate transitions between particular states.

Figure 2. Map of habitat states for 2015. Background grey represents land and white represents water.

Figure 3. Annual habitat state abundances for (a) scrub, (b) flatwoods.

Figure 4. Trends in management effort during periods with available data (a) fire and (b) mechanical cutting.



Habitat state

